

AMAZONIANA	IX	3	281 – 295	Kiel, Dezember 1985
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From cooperation between Max-Planck-Institute for Limnology, Working group "Tropical Ecology", Plön, West Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus – Amazonas, Brazil

Da cooperação entre Max-Planck-Institut für Limnologie, Arbeitsgruppe Tropenökologie, Plön, Alemanha Oc., e Instituto Nacional de Pesquisas da Amazônia, Manaus – Amazonas, Brasil

Foliar nutrient levels of native tree species from Central Amazonia.

2. Campina

by

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(accepted for publication: December 1984)

Abstract

Adult leaves of 14 woody species were sampled in the campina at km 62 of the road Manaus – Caracará. The lamina were classified as to their size and analysed for N, P, K, Ca, Mg and Na.

Comparing the foliar levels of the bioelements to relevant data for other neotropical woody vegetation, they are much below those of forests from geochemically richer areas (Amazon várzea and certain other floodplains, volcanic areas) and resemble the foliar bioelement levels of terra firme vegetation.

Keywords: foliar bioelements, campina, Amazon region, leaf size, tropical forest classification.

Resumen

Se han recolectado hojas adultas de 14 especies leñosas de la campina en el kilómetro 62 de la carretera Manaus – Caracará. Las láminas han sido clasificadas según su tamaño. Seguidamente se las han analizado para N, P, K, Ca, Mg y Na.

Comparando los niveles foliares de bioelementos con datos relativos de otros tipos de vegetación leñosa neotropical, los de la campina son muy inferiores a aquellos de bosques de áreas geoquímicamente más ricas (area de inundación amazónica (várzea) y extra-amazónicas, áreas volcánicas). Son muy semejantes a los niveles foliares de bioelementos de la vegetación de tierra firme.

This study is dedicated to Prof. Dr. Harald Sioli to commemorate his 75th birthday.

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Campina is a low sclerophyllous vegetation growing on 'white sands' (STARK 1970; BRAGA & BRAGA 1975; LISBÔA 1975; KLINGE & MEDINA 1979; ANDERSON 1981). PRANCE & SCHUBART (1978) assume that campina is an old secondary vegetation occupying sites of former white sand forest. Campina is surrounded by campinarana (campina forest, LISBÔA 1975). Campina comprises open or sun campina and closed or shade campina. The difference between these campina types is given by the extent of patches of vegetation separated by barren white sand areas and by the percentage of canopy coverage of the islands (ANDERSON et al. 1975). Each campina type has its own microclimatic characteristics (RIBEIRO & SANTOS 1975). The hydraulic conductivity of the sand is high (REICHARDT et al. 1975). Groundwater and streams draining campina sites are often of the blackwater type (KLINGE 1967; KLINGE & MEDINA 1979; BRINKMANN 1981; St. JOHN & ANDERSON 1982).

In the companion paper KLINGE et al. (1983) have demonstrated that the mean foliar concentrations of N, P, K, Ca, Mg and Na of trees from two stands of várzea forest sensu PRANCE (1979) of the lower Solimões are — also by tropical standards — relatively high. The mean foliar concentrations of the species from an igapó forest sensu PRANCE (1979) of the lower Rio Negro are much lower. The differences between várzea- and igapó foliage are confirmed by the results of chemical analyses of bark and wood samples from the same trees sampled for foliar analysis (KLINGE et al. 1984). A comparison of neotropical foliage chemistry of terra firme forests and of forest growing in floodplains (várzea) has revealed that the former forests in general have rather low foliar bioelement concentrations (KLINGE 1984).

In the present paper foliar concentrations of N, P, K, Ca, Mg and Na of 14 woody species sampled in a campina near Manaus are presented. Their means are compared to other tropical forests.

Material and Methods

The leaves were sampled in the Campina Biological Reserve INPA/SUFRAMA at km 62 of the road Manaus — Caracará from Manaus, in the morning of October 12, 1982.

The list of plant species of that campina comprises 45 species in 35 families (ANDERSON et al. 1975). We sampled 14 species of which according to these authors 7 are common ones, 2 are occasional species, and 3 are rare ones (Table 3). Two species were not classified as to their frequency by ANDERSON et al. *Glycoxylon inophyllum* being dominant in the campina (ANDERSON et al. 1975; LISBÔA 1975) is the only species which was not sampled in the campina proper, but in the transition from campina to campinarana. Ten of the 14 species are included in a study of the dispersal mechanisms of campina species (MACEDO & PRANCE 1978).

The leaves were wrapped in paper and oven-dried at Manaus. The petioles were cut and the leaf blade outlines were drawn on paper, at Plön. By aid of a computer the leaf area was measured. Leaves were not washed or cleaned otherwise prior to chemical analysis. After grinding the powder was oven-dried at 105 °C. Nitrogen was estimated using the Kjeldahl technique. After ashing at 450 °C the samples were treated with conc. HCl. Ca, Mg, K and Na were estimated by flame atomic absorption spectroscopy (Perkin-Elmer AAS 300). P was estimated colorimetrically.

1. Leaf size, Specific leaf area (SLA) and Specific leaf weight (SLW)

Six species (43 %) with leaves between 20.2 and 45 cm² in area are notophylls (WEBB 1960, Table 1). Leaves of four species (29 %) measuring between 45 and 182.2 cm² are mesophylls. Four additional species with leaves between 2.2 and 20.2 cm² are microphylls (RAUNKIAER 1934). The notophyll percentage of the campina is greater than in the igapó forest (KLINGE et al. 1983). An elevated percentage of notophylls was reported by BRUNIG (1974) for kerangas (Heath) forests in East Malaysia, also growing on low nutrient sandy soils. Notophylls are dominant in the bana, South Venezuela (BONGERS et al., in press; CUEVAS & KLINGE, in prep.), the soils being classified as Spodosols (FAO-Unesco 1971 - 1981). They are exposed to drought alternating with waterlogging.

Table 1: Mean specific leaf area (SLA) per leaf size class of 3 Amazon forests.

Forest type	n	Mesophylls (45 - 182.2 cm ²)	n	Notophylls (20.2 - 45 cm ²)	n	Microphylls (2.2 - 20.2 cm ²)	Average
		cm ² /g (1 s.d.)		cm ² /g (1 s.d.)		cm ² /g (1 s.d.)	
Várzea forest ¹⁾	19	124.8 (54.0)a	6	126.7 (35.0)ac	4	167.5 (54.7)ac	139.7
Igapó forest ¹⁾	9	93.6 (19.0)b ^x	8	99.0 (57.2)ab	5	98.7 (49.3)ab	97.1
Campina ²⁾	4	59.4 (9.2)c ^{xx}	6	57.2 (7.8)b ^{xxx}	4	63.2 (24.6)b ^x	59.9

1) KLINGE et al. 1983 2) This study

In each column, figures followed by the same letter are not statistically different (t-test, $p > 0.05$)
 $p < 0.05^x$ $p < 0.01^{xx}$ $p < 0.001^{xxx}$

Acc. to MEDINA (1984) tropical plants growing in highly leached, acid soils low in nutrients have a leaf anatomy characterized by a coriaceous texture, thick cell walls and cuticles, and a compact mesophyll. Their SLA (cm²/g) is lower than the SLA of species growing in more favourable habitats (MEDINA & KLINGE 1983). The mean SLA of the campina species in the three leaf size classes is very low and even lower than in the igapó species growing in low nutrient quartz sand flooded for several month by the Rio Negro (Table 1). The differences between the leaf size classes of each forest are not significant statistically. MEDINA (1984) reported even lower SLA values for bana species (SOBRADO & MEDINA 1980).

The SLW (g/m²) of evergreen species is much greater than of deciduous species (MEDINA 1984). The average SLW values in table 2 increase from 80 g/m² in the várzea forest with a relatively high proportion of deciduous trees (WORBES 1983) to 175 g/m² in the evergreen campina. The differences between the leaf size classes of each forest again are not significant statistically.

Table 2: Mean specific leaf weight (SLW) per leaf size class of 3 Amazon forests.

Forest type	Mesophylls		Notophylls		Microphylls		Average
	n	g/m ² (1 s.d.)	n	g/m ² (1 s.d.)	n	g/m ² (1 s.d.)	
Várzea forest ¹⁾	19	83.8 (27.9)a	6	84.1 (23.0)a	4	75.6 (22.9)a	81.2
Igapó forest ¹⁾	9	110.7 (21.2) ^{bxx}	8	129.3 (60.5)ab	5	115.2 (34.8)ab	118.4
Campina ²⁾	4	171.6 (27.4) ^{cxxx} d ^{xxx}	6	177.9 (26.7) ^{bxxx}	4	179.6 (73.3) ^{b^x}	176.4

1)KLINGE et al. 1983

2)This study

For statistical differences see note in table 1.

2. Foliar levels of N, P, K, Ca, Mg and Na

2.1. Concentrations per unit dry weight

The foliar concentrations of N, P, K, Ca, Mg and Na of the campina species are tabulated in table 3. The species are arranged acc. to their leaf size. There is no statistically significant difference between the means of the leaf size classes, except for Ca. The mean Ca concentration of the mesophylls is significantly higher than is the mean concentration of Ca in the notophylls.

The variability of all elements within the mesophylls is relatively low. This is shown by the coefficient of variation. It is relatively small in the mesophylls, increases considerably among the notophylls, and is usually highest in the microphylls.

2.2. Content per unit leaf area

The foliar bioelement contents expressed as g/m² are tabulated in table 4. While there is no statistical difference between the contents of N, P, K and Mg of the three leaf size classes, the Ca content of the mesophylls is significantly higher than in both other leaf size classes, and the Na content of the notophylls is significantly higher than the Na content of the mesophylls. The coefficient of variation also increases from the mesophylls towards the microphylls, but the increase is usually not as strong as in the absolute concentrations (Table 3).

Comparing the nitrogen and phosphorus contents of the campina species to those reported by MEDINA (1984) for deciduous (1.6 g N/m², 0.12 g P/m²) and evergreen species (4.3 g N/m², 0.23 g P/m²), of a dry tropical forest the campina species (1.9 g N/m², 0.1 g P/m²) resemble the deciduous species.

2.3. N/P ratio

High N/P ratios are indicative of a restricted soil phosphorus supply (MEDINA 1984). Only four campina species present N/P ratios below 20 : 1 (Table 4). The same small proportion of low N/P ratios was observed in the igapó community (KLINGE et al. 1983). Because of the high standard deviation of the mean N/P ratio of the campina species it is not significantly different from the mean N/P ratio of the várzea forest with much higher foliar bioelement concentrations and with smaller N/P ratios than both the campina and the igapó, respectively.

2.4. Foliar alkali- and alkali-earth metals

Hydrochemical research in the Amazon region (FURCH 1976, 1984; FURCH & KLINGE 1978; FURCH et al. 1982; JUNK & FURCH 1980) has revealed that chemically poor waters present a dominance of alkali metals over the alkali-earth metals. In the chemically richer Solimões water, however, the ratio between both elemental groups is reversed. In the comparative study of foliage chemistry of inundation forests in Central Amazonia (KLINGE et al. 1983) corresponding differences between tree species from both inundation forest types were observed.

The concentrations of alkali-earth- and alkali metals in the campina foliage, together with the relative contribution of these elements to their sum, are presented in table 5. A general dominance of the alkali- over the alkali-earth metals is observed. The ratio of both groups of elements, however, is only 1.1 : 1 in the mesophylls, while it is 2 : 1 in the notophylls and microphylls, respectively.

There is a single species (*Miconia* sp.) whose foliage is dominated by Ca. 57 % of the species present a dominance of foliar potassium, while 36 % of the species present a dominance of foliar sodium.

The mean concentration of foliar sodium of the campina is surprisingly high (Table 3). It is even 2.4 times higher than the already high foliar Na concentration of the Low bush savanna in Surinam (1800 ppm, STARK 1970). It is noteworthy that the foliage of the mixed terra firme forest at Manaus is also high in Na (1146 ± 827 ppm, GOLLEY et al. 1980). Although extremely high the foliar Na concentration of the campina does by far not reach the Na concentration of halophytes (25000 - 154000 ppm, FLOWER & LÄUCHLI 1983) or of grasses and herbs (up to 8400 ppm, BAUMEISTER & ERNST 1978). Since it cannot be excluded with certainty that the campina leaves were contaminated by sweat during the sampling (October 12, 1982 was a very hot and sunny day) the potential impact of sweat was checked. We assumed two drops of sweat per each leaf. Acc. to RÖMPP (1975) sweat usually contains over 0.5 % NaCl. Two drops of sweat (0.1 ml) containing then 0.4 mg Na were assumed to have contaminated each leaf sampled. The calculations, separately for the three leaf size classes, however, show that, if contamination by sweat occurred, it accounts for only a minor portion of the Na concentration of the campina leaves and cannot explain the observed foliar Na concentration in the order of 1000 to 18000 ppm Na (Table 3).

3. Foliar bioelements of the campina, in comparison with other tropical forests

Comparing the mean values of the six foliar elements of the campina vegetation to those of other tropical forests (Table 6), it can be expected from the outset that the várzea foliage or the foliage of forests growing on chemically rich soils is richer in bioelements than the campina. This expectation is realized by the data for the várzea forest and the Moist Tropical Forest of Panama (Table 6). The dry forest and partially the semideciduous forest, too, have also higher foliar bioelement concentrations.

The forests listed below the campina, although differing in one or another foliar bioelement from the campina, are much similar to the latter and their relatively low foliar bioelement concentrations contrast markedly to those of the first four examples in table 6.

Tab. 3: Concentration of foliar bioelements of 14 campina species.

Species	Family	Abundance ¹⁾	Dispersal mechanism ²⁾	ppm						
				Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Sodium	
<i>Miconia</i> sp.	Melastomataceae	?		9300	410	4150	5270	3140	1160	
<i>Clusia</i> sp.	Clusiaceae	?		10400	680	8890	7990	2580	3370	
<i>Glycoxylon inophyllum</i> (Mart. e Miq.) Ducke	Sapotaceae	+++	O	8900	590	9160	4570	3130	3010	
<i>Macrobolium arenarium</i> Ducke	Leguminosae	(+)		13000	380	7320	5570	1870	1940	
				Mean	515	7380	5850	2680	2370	
				s.d.	584 a	2301 a	1595 a	600 a	1010 a	
				s.d. %	5.6	31.2	27.3	22.4	42.6	
<i>Pagamea duckei</i> Standl.	Rubiaceae	+++	O	10900	470	8650	3780	3240	2550	
<i>Ouratea spruceana</i> Engl.	Ochnaceae	+++	O	8300	380	6666	1590	2310	2210	
<i>Manilkara amazonica</i> (Huber) Standl.	Sapotaceae	+		9000	520	3380	1200	1680	5160	
<i>Mouriri nervosa</i> Pilg.	Melastomataceae	(+)	O	10700	450	3110	1100	2230	5890	
<i>Hirtella racemosa</i> Lam. var. <i>racemosa</i>	Chrysobalanaceae	+++	O	9400	300	3840	4840	2800	6490	
<i>Mabea occidentalis</i> Benth.	Euphorbiaceae	+++	Au	13600	840	8290	1800	1740	2910	
				Mean	10317	493	5656	2333	4202	
				s.d.	1893 a	186 a	2682 a	1549 b ^x	605 a	
				s.d. %	18.3	37.7	47.4	64.9	25.9	
<i>Sandemaniana hoeheii</i> (Cogn.) Wurdack	Melastomataceae	+++	O	7900	380	4610	2340	3430	210	
<i>Tabernaemontana rupicola</i> Benth.	Apocynaceae	+++	Au	13500	110	4660	1990	3010	3210	
<i>Eugenia patrisii</i> Vahl	Myrtaceae	(+)	D	6100	300	3940	2980	1630	3640	
<i>Vernonia grisea</i> Baker	Compositae	+	An	24300	900	15470	6740	4230	18580	
				Mean	12950	423	7170	3513	3075	
				s.d.	8197 a	338 a	5543 a	2190 ab	1088 a	
				s.d. %	63.3	79.9	77.3	62.3	35.4	

For statistical differences see note in Table 1

1) Acc. to ANDERSON et al. (1975);

common occasional rare

+++ +

2) Acc. to MACEDO & PRANCE (1978);

Anemochory Autochory Dyszoochory Ornithochory

An Au D O

Tab. 4: Foliar contents of N, P, K, Ca, Mg and Na (g/m²) in 14 campina species.

Species	N	P	K	Ca	Mg	Na	N : P
<i>Miconia</i> sp.	1.403	0.062	0.626	0.795	0.474	0.175	22.6
<i>Clusia</i> sp.	1.537	0.101	1.314	1.181	0.381	0.498	15.2
<i>Glycoxylon inophyllum</i>	1.830	0.121	1.505	1.145	0.384	0.399	15.1
<i>Macrobolium arenarium</i>	2.366	0.069	1.332	1.014	0.340	0.353	34.3
Mean	1.784	0.088	1.194	1.034	0.395	0.356	21.8
s.d.	0.427 a	0.028 a	0.388 a	0.175 a	0.057 a	0.135 a	9.0 a
s.d. %	23.9	31.8	32.5	16.9	14.4	37.9	41.3
<i>Pagamea duckei</i>	1.687	0.073	1.339	0.585	0.502	0.395	23.1
<i>Ouratea spruceana</i>	1.521	0.070	1.220	0.291	0.423	0.405	21.7
<i>Manilkara amazonica</i>	2.022	0.117	0.759	0.270	0.377	1.159	17.3
<i>Mouriri nervosa</i>	2.018	0.085	0.587	0.207	0.421	1.111	23.7
<i>Hirtella racemosa</i>	1.755	0.056	0.717	0.904	0.523	1.212	31.3
<i>Mabea occidentalis</i>	2.119	0.131	1.292	0.280	0.271	0.453	16.2
Mean	1.854	0.087	0.986	0.423	0.420	0.789	22.2
s.d.	0.234 a	0.029 a	0.333 a	0.270 b ^{xx}	0.091 a	0.409 b ^x	5.4 a
s.d. %	12.6	33.3	33.8	63.8	21.7	51.8	24.3
<i>Sandemaniana hoeheii</i>	1.689	0.081	2.138	0.500	0.733	0.045	20.9
<i>Tabernaemontana rupicola</i>	1.566	0.013	0.541	0.231	0.349	0.372	120.5
<i>Eugenia patrisii</i>	1.626	0.080	1.050	0.794	0.435	0.970	20.3
<i>Vernonia grisea</i>	2.960	0.110	1.884	0.821	0.515	2.263	26.9
Mean	1.960	0.071	1.403	0.587	0.508	0.913	47.2
s.d.	0.668 a	0.041 a	0.739 a	0.278 b ^{xxx}	0.165 a	0.978 ab	49.0 a
s.d. %	34.1	57.7	52.7	47.4	32.5	107.1	103.8
Overall mean	1.864	0.084	1.165	0.644	0.438	0.701	29.2
s.d.	0.414	0.031	0.486	0.351	0.111	0.586	26.9
s.d. %	22.0	36.9	41.7	54.5	25.3	83.6	92.1

For statistical differences see note in Table 1

Tab. 5: Concentrations of foliar alkali-earth- and alkali metals and the proportions of Ca, Mg, K and Na.

Species	ppm		K + Na		%			
	Ca + Mg	K + Na	Ca + Mg	Na	Ca	Mg	K	Na
Mesophylls	13720	0.63 : 1	38.4	22.9	30.2	8.5		
	22830	1.16 : 1	35.0	38.9	38.9	14.9		
	19870	1.58 : 1	23.0	15.8	46.1	15.1		
	16700	1.24 : 1	33.4	11.2	43.8	11.6		
	18280	1.14 : 1	32.5	15.3	39.8	12.5		
s.d.	3938 A		6.6 ACa	5.5 AB ^{xx} c	7.0 Aad ^{xx} e	6.9 AB ^{xx} fxx		
Notophylls	18220	1.60 : 1	20.7	17.8	47.5	14.0		
	12776	2.28 : 1	12.5	18.1	52.2	17.3		
	11420	2.97 : 1	10.5	14.7	29.6	45.2		
	12330	2.70 : 1	8.9	18.1	25.2	47.8		
	17970	1.35 : 1	26.9	15.6	21.4	36.1		
s.d.	14740	3.16 : 1	12.2	11.8	56.2	19.7		
Microphylls	14576	2.09 : 1	15.3	16.0	38.7	30.0		
	2935 A		7.0 B ^{xx} a	2.5 Aac	15.0 AB ^x de	14.9 B ^x ae		
	10590	0.84 : 1	22.1	32.4	43.5	2.0		
	12870	1.57 : 1	15.5	23.4	36.2	24.9		
	12190	1.64 : 1	24.4	13.4	32.3	29.9		
s.d.	45020	3.10 : 1	15.0	9.4	34.3	41.3		
Overall mean	20168	2.06 : 1	19.3	19.7	36.6	24.5		
	16596 A		4.7 B ^x Da	10.3 Aac	4.9 AB ^{xx} d ^x	16.5 AB ^{ad}		
	17232	1.71 : 1	21.3	16.9	38.4	23.4		
	8581		9.5	6.1	10.3	14.4		

For statistical differences see note in Table 1

Mayusculs refer to columns, minusculs to rows

4. Tentative classification of tropical forest based on foliar bioelements

In search for a scale of a classification of foliar bioelement concentrations, the absolute ranges of foliar N, P, K, Ca, Mg and Na of Amazon inundation forests were divided in four equal portions. Each species was then compared to the respective four concentration classes, and species with a similar bioelement pattern were identified (KLINGE et al. 1983). For example, species with concentrations of foliar N, P, and K in both upper concentration classes, but with foliar Ca, Mg and Na in the lower concentration classes were classified as 'rich to very rich in foliar N, P, and K, and low to very low in foliar Ca, Mg and Na'.

The next step was to compile chemical foliage data of tropical forests. The obtained ranges of the various foliar bioelements were considered as the respective tropical standards against which individual data were measured. This allowed to classify the várzea forests as 'relatively rich by tropical standards' in foliar bioelements, while the igapó forest was classified as 'relatively poor in these elements by tropical standards' (KLINGE et al. 1983).

In a study of exclusively neotropical forests with a majority of examples from Amazonia (KLINGE 1984), two chemical groups of forest foliage were established. One group had significantly higher concentrations of foliar N, P, K, Ca and Mg than the other one. The group with lower concentrations comprised terra firme forests and also the igapó forest. The group with higher concentrations was composed by várzea forests and a few extra-Amazonian forests in Panama and western Venezuela. Both areas are geochemically richer than most of the Amazon region (FITTKAU 1971), the minor portion of Amazonia which is geochemically relatively rich, being the várzea. Comparing the foliar means of both groups to the tropical foliar standards subdivided in three equal sections (upper portion termed 'rich by tropical standards', middle portion accordingly as 'medium by tropical standards', and lower portion as 'poor by tropical standards') (Fig. 1), it is evident that even the group with higher foliar concentrations has mean concentrations of foliar Ca, K, Mg and P which are 'medium by tropical standards', while the group of lower concentrations is in these elements 'poor by tropical standards'. The mean foliar nitrogen concentration of the group of higher concentrations, however, is identified as 'rich in foliar N, by tropical standards', and the mean nitrogen concentration of the other group as 'medium in this bioelement, by tropical standards'.

In Fig. 2, the foliar concentrations of the sixteen stands (Table 6 refers) are presented graphically. They are compared, individually for each element, to both the levels of foliar concentrations of the groups of higher and lower concentrations, and to the respective tropical standards. While most forests including the campina are in all elements, except for sodium, in the lower portion of the tropical ranges, the first three forests of table 6 fall in the middle portion in the cases of foliar Ca, K and Mg. The foliar N concentration of the várzea forests falls in the upper portion of the tropical range and is accompanied by the foliar N concentration of the Brazilian podzol vegetation (no. 15, Table 6). The Tall Caatinga and the Low bush savanna have foliar Mg concentrations classified as 'medium by tropical standards' while they are classified as 'poor by tropical standards' in the remaining foliar elements. There are also some additional exceptions from the general rule which are not mentioned specifically.

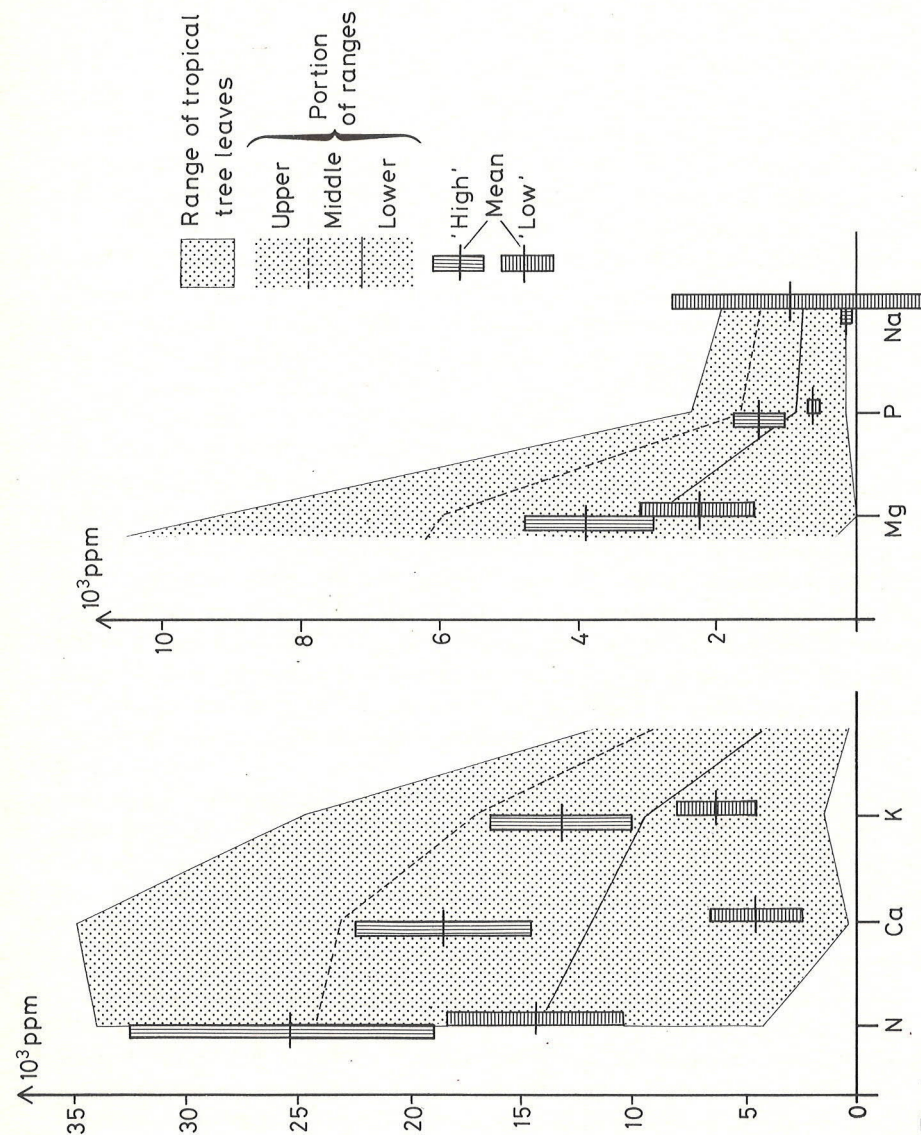


Fig. 1: 'High' and 'low' mean foliar concentrations of N, P, K, Ca, Mg and Na of neotropical (mostly Amazonian) forests, in comparison with the ranges of these elements in tropical tree foliage subdivided in three equal sections (upper, middle and lower ones, defined as - by tropical standards - 'rich', 'medium' and 'poor').

Tab. 6: Average foliar bioelement levels of selected tropical forest stands.

Forest type	N of species	ppm (1 s.d.)							Source
		N	P	K	Ca	Mg	Na		
1. Várzea forest	28	25865	1755	13183	19141	3982	195	KLINGE et al. 1983	
Marchantaria		(5307) b ^{xxx}	(430) b ^{xxx}	(6840) b ^{xxx}	(8312) b ^{xxx}	(1850) b ^{xx}	(270) b ^{xx}		
2. Moist tropical f.	?	14000	1500	15300	22900	2575	225	GOLLEY et al. 1975	
Panama			(931) c ^{xx}	(6230) c ^{xxx}	(1824) c ^{xxx}	(340) a	(126) c ^{xx}		
Dry forest									
3. Deciduous sp.	7	21000	1580	17000	15800	3600	n.d.	MEDINA 1984	
		(2700) c ^{xxx}	(300) d ^{xxx}	(8100) d ^{xxx}	(8800) d ^{xxx}	(1800) a			
4. Evergreen sp.	4	11800	710					MEDINA 1984	
		(1600) a	(70) c ^{xx}						
Semideciduous f									
5. Deciduous sp.	4	17100	1150	6581	7700	2900	n.d.	MEDINA 1984	
		(2200) d ^{xx}	(460) f ^x	(2900) a	(3600) e ^x	(1600) a			
6. Evergreen sp.	9	12100	570					MEDINA 1984	
		(4700) a	(200) a						
7. Campina (BS)	14	11093	479	6581	3697	2644	4309	This study	
		(4376) a	(216) a	(3386) a	(2184) a	(774) a	(4436) a		
8. Montane forests	21	11730	660	5133	7230	1960	n.d.	MEDINA 1984	
		(1850) a	(143) g ^{xx}	(351) a	(825) f ^{xxx}	(551) c ^{xx}			
9. Amazon forest	27	10560	610	5730	4030	1300	n.d.	MEDINA 1984	
		(2800) a	(115) h ^x	(987) a	(1976) a	(265) d ^{xxx}			
10. Heath forest (BS)	9	8702	219	3507	7497	1995		PEACE & MacDONALD 1981	
		(1373) a	(62) i ^{xxx}	(1484) e ^{xx}	(5082) g ^x	(2222) a		KLINGE et al. 1983	
11. Igapó forest (BS)	22	17305	618	6325	2506	1218	249	HERRERA 1979	
		(4042) e ^{xxx}	(256) a	(2617) a	(2041) a	(584) e ^{xxx}	(441) d ^{xx}		
12. Tall Caatinga (BS)	40	10820	560	5280	5830	3560	n.d.	STARK 1970	
		(4090) a	(180) a	(2820) a	(3830) a	(1560) f ^{xx}			
13. Dimorphandra f.	1	20410	1375	1548	8000	2400	500	STARK 1970	
Surinam (BS)								STARK 1970	
14. Low bush sand savanna (BS)	?	5050	625	1547	6800	3750	1800	STARK 1970	
15. Brazil podzols (BS)	?	28200	2500	6500	2500	2200	240	STARK 1970	
16. Bana (BS)	12	8350	440	6950	3510	n.d.	n.d.	SOBRADO & MEDINA 1980	
		(3452) a	(174) a	(3512) a	(1575) a				

¹Numbers refer to Fig. 2

BS = Bleached sand and similar extremely low nutrient soils, partly classified as Spodosols
For statistical differences see note in Table 1

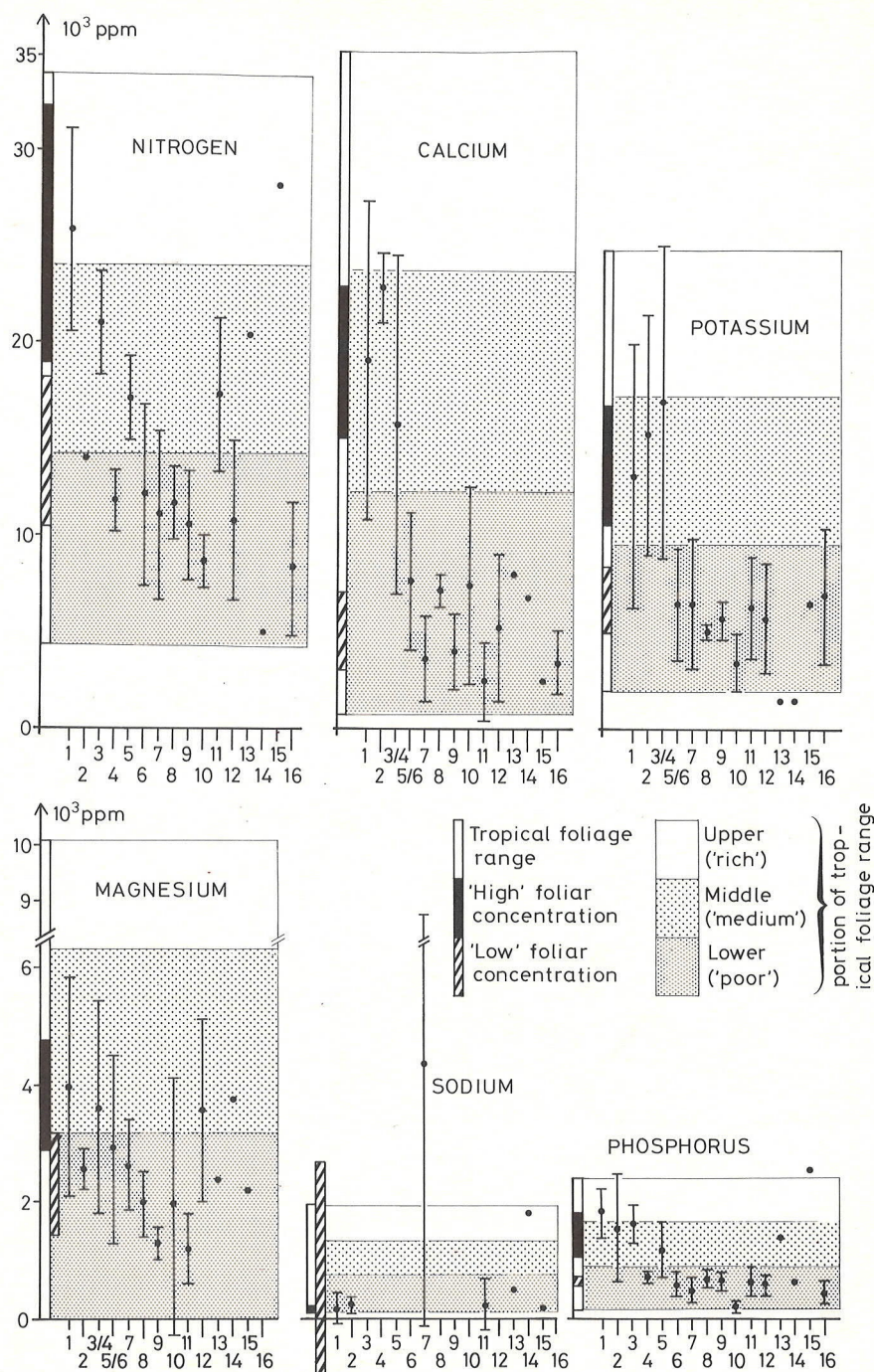


Fig. 2:
Mean foliar concentrations of N, P, K, Ca, Mg and Na of 16 tropical forests identified in table 6, in comparison with both the respective tropical ranges subdivided in three equal portions (upper or 'rich', middle or 'medium', lower or 'poor'), and 'high' and 'low' mean foliar concentration of neo-tropical forests (see Fig. 1).

Final remarks

Oligotrophic bleached quartz sands whether or not classified as Spodosols are widespread in the humid tropics of particularly South America and Southeast Asia (KLINGE 1968). The Rio Negro basin in northern South America is one of the centres of distribution of these soils (KLINGE 1966).

One peculiarity of these soils is that they carry a vegetation which regarding floristics and structure differs strikingly from the surrounding forest on heavier textured soils (SPRUCE 1908; DUCKE & BLACK 1953; STEENIS 1935; RICHARDS 1954; BRUNIG 1974). This curious vegetation is intimately related to the 'heath' vegetation (SPECHT 1979).

SIOLI (1954) assumed that the peculiar vegetation of bleached quartz sands is the cause of humic-stained streams of the blackwater-type. Not being a terrestrial ecologist he invited me 25 years ago to join the group of scientists he had gathered in the Max-Planck-Institut at Plön, in order to develop research about the vinculation of land and water, specifically the Amazon blackwaters and their terrestrial environment in which these waters were assumed to rise. Being very grateful for this unique opportunity this paper is dedicated to Harald Sioli at the occasion of his 75th birthday.

Acknowledgments

We are grateful to Dr. S. Renner, University of Hamburg for assistance in sampling and identification of the species; to Dr. H. J. Krambeck, Plön, for measuring the leaf areas, and to D. Albrecht, J. Dieterich, E. Harms, D. Lemcke, all at Plön, and I. Ploog, Schuby, for skillful technical assistance.

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